Automata, matching and foraging behavior of bees

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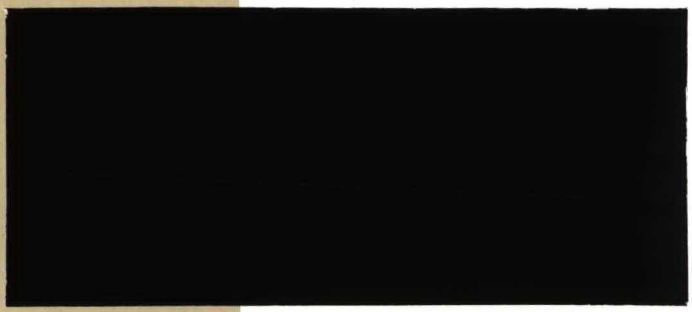

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Automata, Matching and Foraging Behavior of Bees[1]

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Abstract

We discuss two types of simple foraging strategies for bees. Each of these explicit strategies explains that in a multi-bee community the bees will distribute themselves over the nectar sources according to the Ideal Free Distribution. At the same time these strategies explain that in single-bee experimental settings a bee will match, by its number of visits, the nectar supply from the available sources (the Matching Law). Moreover, both strategies explain that in certain situations the bees may behave as if they are risk averse. Our results indicate that a competitive market in a multi-bee community permits individuals to be boundedly rational and still forage optimally.

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1 Introduction

In animal behavior studies many experiments of the following type have been done (Commons et al. 1982, Maynard-Smith 1982, Staddon 1983, Houston 1983, Davison & McCarthy 1988, Menzel & Gregger 1992). An animal subject can repeatedly choose from two different food sources that give precisely the same quantity of the same food, however with different frequencies. Suppose that, at each point in time, the yellow source Y gives one unit of food with probability p, and the blue source B gives one unit of food with probability q (and 0 units otherwise). These experiments reveal that the animal subject behaves as if, asymptotically, it matches the reward probabilities by the frequencies of visiting the alternatives, i.e. the number of visits to Y relates to the number of visits to B as p to q (cf. Staddon 1983, Houston & Sumida 1987, Krebs & Kacelnik 1991, Menzel & Gregger 1992). This kind of behavior has been called "the Matching Law" (see for example Houston 1983, Krebs & Kacelnik 1991).

These single-animal experiments are closely related to so-called two-armed bandit problems in statistical decision theory, where a player wishes to maximize his profits from playing a two-armed gambling machine of which one arm gives a greater probability of winning. The rational player, not knowing the winning probabilities of the arms, should try to find the more profitable arm and play it exclusively (DeGroot 1970, Rotschild 1974). A behavior of matching the succes probabilities seems to be irrational (Houston et al. 1982, Staddon 1983, Real 1992). One of our goals is to explain this "irrational" behavior by presenting simple foraging strategies that are optimal and rational in a multi-animal natural environment.

We show that in a multi-animal setting these strategies lead to what is known as the Ideal Free Distribution (IFD, Fretwell 1972, Milinski & Parker 1991). Peleg & Shmida (1992) have proved the existence of the IFD in a general framework of an environment with many flower types and

bee types. To explain briefly the IFD, consider n (identical) animals and two food sources Y and B where food is being supplied with rates p and q respectively. Then after some time a fraction $p/(p+q)$ of the n animals will be feeding at the Y source while a fraction of $q/(p+q)$ will be at B. Thus, the number of animals at Y relates to the number of animals at B as p to q. In a natural multi-animal situation, establishing the IFD seems to be the rational thing to do, since at the IFD the average intake of food is the same at all food sources. The population is at equilibrium; no animal can improve its payoff by feeding at another food source. When non-cooperatively trying to establish the IFD is the "natural" thing to do for the animal, then in an artificial single-animal setting one may observe irrational behavior.

When applying our strategies to a situation where the animal can choose between two probabilistic food sources in which the food supply is normally distributed with the same mean but with different variances, our result shows that the animal will act as if it is risk averse or, as if it is risk prone (sensu Real & Caraco 1986). An animal will act as if it is risk averse if its (individual) critical level is smaller than the mean, and risk prone otherwise. Here the critical level is a threshold by which the animal judges each quantity of food it obtains as being satisfactory or not. The animal will prefer the food source with the smallest probability of getting something below critical level.

For simplicity we shall talk about bees instead of animals in this paper. Most of the wild bees, especially in the Mediterranean area, are solitary bees which live about four-five weeks (Shmida et al. 1993). Each female has its own nest and raises its brood alone. There is no exchange of foraging information among bees. Each bee is assumed to be a maximizer of Darwinian fitness (Hammerstein & Selten 1993), i.e. it maximizes its average nectar intake per time unit. Nectar will be considered as the only reward for

the bee in the model. Nectar is produced by flowers for the sole purpose of attracting pollinators. Bees have no innate preference to particular flowers (Heinrich 1979, Menzel 1985, 1990, Menzel & Shmida 1992) and their foraging patterns appear to be influenced by experience. Experiments reveal that bees use mainly their short-term memory for decision-making in local flower patches (Menzel & Gregger 1992) and take into account only the last one or two flowers in the process of deciding on leaving or staying in a patch of a given flower type (Real et al. 1990, Cresswell 1990, Real 1991, 1992, Kadmon & Shmida 1992, Kadmon et al. 1992). The above experimental result initiated our approach to assume that the bees have bounded recall. The strategies we provide are described by finite automata (Ben-Porath & Peleg 1987) by which the bees respond only to their own payoffs and remember only payoffs of the last few visits. In this paper we neither include travel times nor handling times for the flower types. These parameters are considered in some other models (Laverty 1980, Harder 1987, Friedman & Shmida 1992, Peleg & Shmida 1992).

The two explicit strategies examined in this paper shall be called *the ϵ-sampling strategy* and *the failures strategy*. Briefly one could say that the ϵ-sampling strategy is to visit one alternative repeatedly, but every now and then sampling on the other alternative and to switch if the other alternative is better than the one previously selected. The failures strategy describes an innate behavior leading to matching according to some simple finite automaton (e.g. leave Y after y empty flowers, leave B after b empty flowers). The two behavioral strategies represent two alternative approaches to model choice rules of foraging animals: resource dependent moves vs. resource independent moves. These strategies will be discussed in sections 2 and 3 respectively, each with respect to multi-animal and single-animal settings and in relation to risk. Section 4 concludes with some discussion on related literature.

To simplify notations we restrict our attention to the situation where there are only two food sources: Y (yellow) and B (blue). However, our results can be extended to situations with any finite number of food sources.

2 The ϵ-Sampling Strategy

The ϵ-sampling strategy is briefly described as follows. A foraging bee which has to choose between two colored resources will use the following rule: initially choose one of the colors at random, then at each point in time stay at the current color with probability $1-\epsilon$ and sample the other color with probability ϵ; when sampling, if you find a payoff above your critical level, then switch to this new color, otherwise return to the previous color immediately; at this next color (new or old) again at each point in time stay with probability $1-\epsilon$, sample elsewhere with probability ϵ. This ϵ-sampling strategy is close to Heinrich's (1979) idea of "Major-Minor behavior" of bees, which motivated our research.

Definition 2.1 *Let $\alpha, \epsilon \in (0,1)$, let $a(t) \in \{Y, B\}$ represent the action selected and let $r(t) \in \mathbf{R}$ be the payoff at time $t \in \{1,2,3,\ldots\}$.*
Define $cl(1) = 0$ and

$$cl(t+1) = \alpha cl(t) + (1-\alpha)r(t) \tag{1}$$

for $t \geq 1$. Then $cl(t)$ is called the critical level at time t.
Let Y_ϵ denote the mixed action: choose Y with probability $1-\epsilon$ and B otherwise and let B_ϵ be defined similarly.
The ϵ-sampling strategy is defined by playing:
at $t = 1$ use $Y_{0.5}$,
at $t = 2$ use $a(1)_\epsilon$,
at $t > 2$ use $a(t-1)_\epsilon$ in case $a(t-1) \neq a(t-2)$ and $r(t-1) > cl(t-1)$, use $a(t-2)_\epsilon$ otherwise.

Note that equation (1) is the linear operator function originally used by Bush & Mosteller (1955). In this definition the parameters α and ϵ are the individual bee's factors. The first one is related to memory and the second one to searching elsewhere. Those familiar with game theory can think of

ε as a bee's *trembling hand* (Selten 1975) trying to play a pure action. We wish to emphasize that different individuals may have different parameters, but our results remain the same.

Let $\mathbf{N}$ denote the set of natural numbers $\{1, 2, 3, \ldots\}$. Then, consider what happens if we have a population of $n \in \mathbf{N}$ bees that are foraging on two patches of flowers, a yellow patch Y and a blue patch B. Per unit of time the yellow patch has a total nectar supply of $y \in \mathbf{R}_+$, while there is a total quantity of $b \in \mathbf{R}_+$ at patch B. We make the following assumptions:

a. If at some stage $t \in \mathbf{N}$ there are n_Y bees at Y, then we assume that at this stage each of these bees is receiving $r(t) = y/n_Y$ units of nectar. This means that the total quantity of nectar at Y is being equally distributed over the visiting bees at Y at each stage. Likewise for B.

b. There is no accumulation of nectar at a patch. All nectar is taken by the bees at each stage and if at some stage there are no bees at a patch then at the next stage the total quantity is still the same.

c. The bees sampling factors ε are sufficiently close to 0 to have a negligible probability of two or more bees moving at the same time. Thus the distribution of bees over flower types changes by one bee moving either from Y to B or from B to Y. (Here "moving from Y to B" means: previously the bee was at Y, now it has gone to B for a sample and since the payoff received at B is larger than the critical level it decides to stay at B.)

d. We assume that, when going out sampling, the bee has been in Y sufficiently long to have its critical level close to y/n_Y.

Theorem 2.2 *Under the above assumptions the population will stabilize in the Ideal Free Distribution.*

Proof: Firstly, observe that, due to its ε, each bee will go out sampling the other color infinitely often. Hence, if the process stabilizes in some distribution of bees over Y and B, then it must be such that no single bee can strictly improve its payoff by moving to the other color. Secondly, observe that whenever a bee moves from Y to B we must have that $y/n_Y < b/(n_B+1)$, where n_Y and n_B are the numbers of bees before the move at Y and B respectively.

We now define a *potential function* (Monderer & Shapley 1988) on the distributions of bees as

$$P(n_Y, n_B) = y \sum_{m=1}^{n_Y} 1/m + b \sum_{m=1}^{n_B} 1/m, \tag{2}$$

where $\sum_{m=1}^{0} 1/m$ is understood to be equal to 0. If a bee moves from Y to B, then the distribution changes from (n_Y, n_B) to $(n_Y - 1, n_B + 1)$. At the same time the potential changes from $P(n_Y, n_B)$ to $P(n_Y - 1, n_B + 1)$. Now $P(n_Y - 1, n_B + 1) - P(n_Y, n_B) = b/(n_B + 1) - y/n_Y > 0$ because the bee decided to stay at B. Hence, with each bee movement the potential strictly increases. Since there are only finitely many distributions of the n bees and since the bees will keep moving as long as possible, the potential function will eventually reach its maximum. At this maximum we have that $y/n_Y \geq b/(n_B+1)$ and $b/n_B \geq y/(n_Y+1)$; hence

$$y/n_Y \approx b/n_B \tag{3}$$

and the population has reached the IFD. □

We remark that the stable situation that arises from all bees doing ε-sampling strategies, needs not be Pareto-optimal. Take for example 4 bees, 8 units of nectar at Y and 1 unit of nectar at B. For this situation the IFD will be that all 4 bees will go to Y and the 1 unit at B is not being consumed. Thus each bee is getting a payoff 2 all the time. The bees could all improve their payoffs by visiting B in turns, giving each bee the

average payoff $9/4 > 2$. For a continuum of bees the distribution obtained from the ε-sampling strategies will indeed be Pareto-optimal, so that in a natural environment with many bees and flowers the IFD solution obtained is practically Pareto-optimal.

It should be noted that, to derive the IFD result of Theorem 2.2 one can also take the alternative potential function P' defined by

$$P'(n_Y, n_B) = \min\{y/n_Y, b/n_B\} \tag{4}$$

for $n_Y \neq 0$ and $n_B \neq 0$, while $P'(0, n_B) = b/n_B$ and $P'(n_Y, 0) = y/n_Y$. Using this alternative potential function one can even show that a population of ε-sampling bees with different sizes will stabilize in the IFD. Here we assume that a bee of size i consumes i times as much nectar as a bee of size 1. Correspondingly, one should think of n_Y and n_B as the total size of all bees present at Y and B respectively. If we have a finite number of bees with sizes in $[1, k]$, where k is the maximum size present, then the population has the IFD if and only if $y/n_Y \geq b/(n_B + i)$ and $b/n_B \geq y/(n_Y + j)$, where i (j) is the smallest size present at Y (resp. B). Notice that, if $n_Y \neq 0$ and $y/n_Y < b/(n_B + i)$, then $y/(n_Y + j) < y/n_Y < b/(n_B + i) < b/n_B$ implying that no bee will move from B to Y. On the other hand, a bee of size i sampling from Y at B would decide to stay at B. There is at least one bee of size i at Y and hence, by the ε-sampling strategy at least one bee will move from Y to B. Suppose that it has size $x \geq i$. Then the distribution changes from (n_Y, n_B) to $(n_Y - x, n_B + x)$ and $P'(n_Y - x, n_B + x) = \min\{y/(n_Y - x), b/(n_B + x)\} > y/n_Y = \min\{y/n_Y, b/n_B\} = P'(y/n_Y, b/n_B)$. Hence, with each moving bee P' is strictly increasing and the process will reach a (local) maximum after finitely many moves. At this (local) maximum the population is in IFD. Remark that, if all bees have the same size, then every local maximum of this alternative potential function P', as of the original potential function P, is necessarily a global maximum.

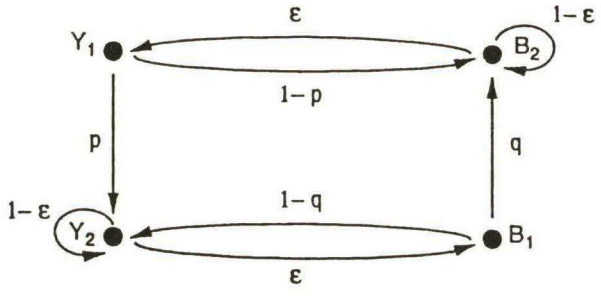

Figure 1: Markov chain for the ε-sampling strategy

Let us now see what happens if we take a single bee for an experiment of the following type (Figure 1). We have two artificial *Bernoulli flowers* Y (yellow) and B (blue). Each time the bee visits the yellow flower it will receive 1 unit of nectar with probability p and 0 units otherwise. Equivalently, in a natural situation one can think of a patch of yellow flowers, where a p-fraction of the flowers is full, while a $(1-p)$-fraction is empty. For the blue flower we have probability q for a full flower. Let, as before, ε be the bee's sampling factor. We assume that when sampling from Y to B the bee's critical level will approximately be p and when sampling from B to Y it will approximately be q. If the bee applies the ε-sampling strategy, then its behavior corresponds with the Markov chain depicted in Figure 1. In this figure Y_1 and B_1 correspond to the sampling stages at the respective colors; one gets there by sampling probability ε and one decides to remain (or else to return) with probability p and q respectively. Consequently, Y_2 and B_2 represent situations where the bee has decided to stay in the particular color.

Computing the stationary distribution of this Markov chain, one finds that the number of visits to Y relates to the number of visits to B as $p + q\varepsilon$

to $q + p\epsilon$, that is approximately as p to q if ϵ is small. Thus we have the following theorem.

Theorem 2.3 *A bee applying the ϵ-sampling strategy in a single-bee experiment will exhibit matching the payoff probabilities by the frequency of its visits (the Matching Law).*

Attitude Towards Risk

Consider a single bee foraging on two patches Y and B, in which all flowers have a normally distributed nectar supply with a common mean μ, but where the distributions differ in variance; for the yellow flowers the variance is y while for the blue ones it is b.

Theorem 2.4 *Suppose that the bee is using the ϵ-sampling strategy and has a fixed critical level cl to decide whether any flower is full or empty. Without loss of generality we assume $y < b$.*
If $cl < \mu$, then the bee will act as if it is risk averse, i.e. it will spend more time on Y than on B.
If $cl > \mu$, then the bee will act as if it is risk prone, i.e. it will spend more time on B than on Y.

Proof: If $cl < \mu$, then the probability of getting a reward above the critical level is larger for Y than it is for B (cf. Figure 2). So, when sampling, the bee will decide to move to Y more often than it will decide to move to B. Hence the result. The second part is similar. □

This result can be extended straightforwardly to continuous nectar supply distributions F_Y, F_B on an interval $[\alpha, \beta]$ which have a common mean $\mu = (\alpha + \beta)/2$ and continuous derivatives f_Y, f_B for which

a. $f_i(\mu + x) = f_i(\mu - x)$ for all $x \in [0, \beta - \mu]$ and $i = Y, B$ (which means that f_i is symmetric with respect to the mean μ), and

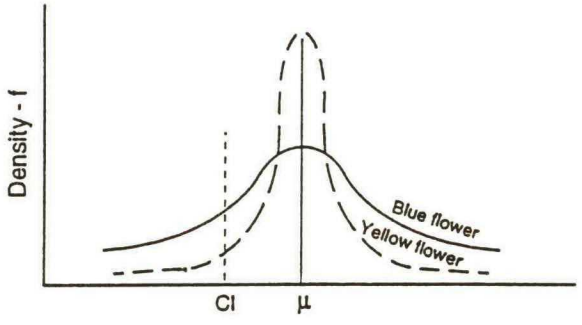

Figure 2: Two patches of flowers with normal nectar distributions

b. there is $x^* \in [0, \beta - \mu]$ with

$f_Y(x) > f_B(x)$ for all $x \in (\mu - x^*, \mu + x^*)$,

$f_Y(x) < f_B(x)$ for all $x \in [\alpha, \mu - x^*) \cup (\mu + x^*, \beta]$.

It should be noted that the result depends on how $F_Y(cl)$ and $F_B(cl)$ are compared. If $F_Y(cl) < F_B(cl)$, then an ε-sampling bee with critical level cl will favour the yellow patch, since $F_i(cl)$ is the probability of having an empty flower at $i = Y, B$. Thus, if F_Y, F_B are nectar supply distribution functions on $(0, \infty)$ with $F_Y(r) < F_B(r)$ for all $r \in (0, \infty)$ (i.e. F_Y strictly dominates F_B according to the "first order stochastic dominance criterion" (Fishburn 1976)), then *every* bee that uses an ε-sampling strategy and judges flowers full or empty according to some critical level, will favour the yellow patch. This means that under these conditions, every bee would visit more yellow flowers than blue flowers or, in other words, spend more than half of its foraging time at the yellow patch.

One can also take nectar distributions as in Figure 3 (or, e.g. negative exponential distributions), in which most flowers are empty or have very small nectar quantities. Such leptokertic distributions are very common in nature (Shreiber 1993, Boker 1993). In case the bee forages on two flower

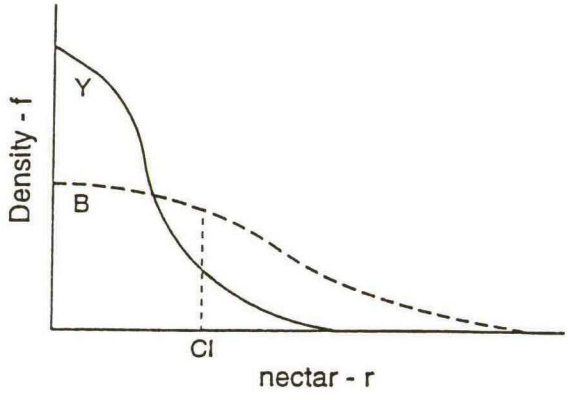

Figure 3: Two patches of flowers with decreasing nectar distributions

patches Y and B with distributions as in Figure 3, then the bee will compare the two patches. If we assume that f_Y and f_B are continuous and cross each other only once (e.g. f_Y starts above f_B), then such a comparison also falls in the first order stochastic dominance. If a bee forages on such flower patches and uses a critical level for switching between Y and B, then it will stay more frequently in the blue patch with the higher variance than in the yellow patch with the lower variance.

We would like to emphasize that the results presented do not depend on ε. All that matters is that $\varepsilon \in (0,1)$ is sufficiently small to have a bee staying in the same patch long enough to get a good estimate of the payoff in this patch. One can even allow ε to be payoff dependent, getting smaller with high current payoffs and getting larger with low current payoffs. The only thing needed is that no matter at what color (patch) the bee is foraging, with probability 1 it will eventually sample at another color (e.g. this condition is satisfied if ε is bounded away from 0). In the multi-bee model the IFD result will still be valid if all individual bees have (sufficiently small) different ε's.

3 The Failures Strategy

In the previous section the bee's "decision" of going out to sample the other color was independent of the payoffs received in the current color; it was determined solely by the innate sampling factor ϵ. In this section we present a foraging strategy which will make the bee move to another color after engaging a certain number of consecutive empty flowers. Recall that empty is to be interpreted as "below critical level". The bee is assumed to behave as a finite automaton (Neyman 1985, Ben- Porath & Peleg 1987, Kalai 1988).

This automaton strategy corresponds to the well known "area- restricted search" (Real et al. 1990) of animal behavior, which was termed "near-far" by Motro & Shmida (1992). The near-far strategy is $A(1,1)$ (see below), a special case of our automaton strategy where the bee uses only the last flower visited to evaluate the current patch. It means: stay in the patch as long as you find food and leave otherwise. Similar strategies have been reviewed by Houston et al. (1982). Experimental studies reveal this near-far behavior (see in Motro & Shmida 1992).

Let us return to the experiment with two artificial flowers Y (yellow) and B (blue) that give 1 unit of nectar with probability p and q respectively (and 0 units otherwise). As already mentioned above, observations indicate that the frequencies of visits by the bee will match these probabilities. The event of receiving 1 shall be called a succes, receiving 0 is a failure.

Definition 3.1 *Let $y, b \in \mathbf{N}$. The finite automaton $A(y,b)$ is given by:*

a. leave Y after y consecutive failures and move to B,

b. leave B after b consecutive failures and move to Y.

As an example we have depicted automaton $A(3,2)$ in Figure 4-a, where Y_k indicates the automaton state of being at Y while the last k consecutive

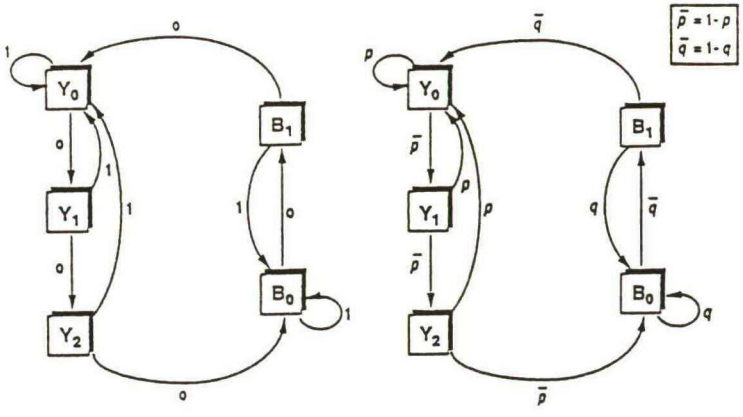

Figure 4: (a) Automaton $A(3,2)$ and (b) related Markov chain

yellow visits were failures ($k = 0, 1, 2$). Obviously B_0 and B_1 are to be interpreted similarly. The automaton corresponds with a Markov chain on the states Y_0, Y_1, Y_2, B_0, B_1, which is depicted in Figure 4-b. In this figure and elsewhere in this paper we write $\overline{p}$ to denote $1-p$ and $\overline{q}$ for $1-q$. This Markov chain in turn corresponds to the transition matrix T given by:

$$T = \begin{array}{c} \\ Y_0 \\ Y_1 \\ Y_2 \\ B_0 \\ B_1 \end{array} \begin{array}{c} \begin{array}{ccccc} Y_0 & Y_1 & Y_2 & B_0 & B_1 \end{array} \\ \begin{pmatrix} p & \overline{p} & 0 & 0 & 0 \\ p & 0 & \overline{p} & 0 & 0 \\ p & 0 & 0 & \overline{p} & 0 \\ 0 & 0 & 0 & q & \overline{q} \\ \overline{q} & 0 & 0 & q & 0 \end{pmatrix} \end{array}$$

If the bee uses $A(3,2)$, then we can compute its frequencies of visits to Y and B by finding the stationary distribution $\pi = (y_0, y_1, y_2, b_0, b_1)$ of T. The frequency of visits to Y is $y_0 + y_1 + y_2$ and that to B is $b_0 + b_1$. The vector π is nonnegative and adding its components gives 1. Furthermore π has the property that $\pi T = \pi$. Using $A(3,2)$ the bee would confirm the matching

law if and only if

$$\begin{cases} y_0 + y_1 + y_2 &= p/(p+q) \\ b_0 + b_1 &= q/(p+q) \end{cases} \tag{5}$$

The equation $\pi T = \pi$ yields

$$y_1 = \overline{p}y_0,\ y_2 = \overline{p}^2 y_0,\ b_1 = \overline{q}b_0 \text{ and } b_0 = (\overline{p}^3/\overline{q}^2)y_0.$$

Hence we find the equations

$$y_0 + y_1 + y_2 = y_0(1 + \overline{p} + \overline{p}^2) = y_0\frac{1-\overline{p}^3}{p},$$

$$b_0 + b_1 = b_0(1+\overline{q}) = b_0\frac{1-\overline{q}^2}{q} = y_0\frac{\overline{p}^3(1-\overline{q}^2)}{\overline{q}^2 q}.$$

So, if we let $f(2,3)$ denote the ratio of the frequencies of visits to Y and B, then

$$f(2,3) = \frac{\text{frequency of visits to } Y}{\text{frequency of visits to } B} = \frac{q\overline{q}^2(1-\overline{p}^3)}{p\overline{p}^3(1-\overline{q}^2)} \tag{6}$$

and the automaton $A(2,3)$ is matching if and only if $f(2,3) = p/q$, which is equivalent to:

$$\frac{p^2\overline{p}^3}{1-\overline{p}^3} = \frac{q^2\overline{q}^2}{1-\overline{q}^2}. \tag{7}$$

Similarly one can show the following theorem.

Theorem 3.2 *The finite automaton $A(y,b)$ matches the payoff probabilities p and q respectively if and only if*

$$\frac{p^2\overline{p}^y}{1-\overline{p}^y} = \frac{q^2\overline{q}^b}{1-\overline{q}^b}. \tag{8}$$

We would like to remark that there are infinitely many $(y,b) \in \mathbf{R}_+^2$ for which (8) holds, because the function $y \mapsto \frac{p^2\overline{p}^y}{1-\overline{p}^y}$ is strictly decreasing on $(0,\infty)$ from ∞ to 0. In fact we have the following result.

Theorem 3.3 *Let $\delta \in (0, 0.5)$ and let $M \in \mathbf{N}$ be such that $(1-\delta)^{M-1} \leq 4\delta(1-\delta^M)$. Then, for all $\delta \leq p \leq q \leq 1-\delta$ there exist $y, b \in [1, M]$ with*

$$\frac{p^2\overline{p}^y}{1-\overline{p}^y} = \frac{q^2\overline{q}^b}{1-\overline{q}^b}.$$

Proof: If $p\overline{p} = q\overline{q}$, then $y = b = 1$ gives the result. Otherwise, assume without loss of generality that $p\overline{p} < q\overline{q}$. Then

$$\frac{q^2\overline{q}^M}{1-\overline{q}^M} = \frac{q\overline{q}\overline{q}^{M-1}}{(1-\overline{q}^M)/(1-\overline{q})} \leq \frac{0.25(1-\delta)^{M-1}}{(1-\delta^M)/(1-\delta)} \leq \delta(1-\delta) \leq p\overline{p}. \quad (9)$$

By continuity there exists $b \in [1, M]$ with $\frac{q^2\overline{q}^b}{1-\overline{q}^b} = p\overline{p} = \frac{p^2\overline{p}}{1-\overline{p}}$. □

For any p, q-situation of yellow and blue flowers with $p, q \in [\delta, 1-\delta]$ this theorem provides the existence of real numbers $y, b \in [1, M]$ for which $\frac{p^2\overline{p}^y}{1-\overline{p}^y} = \frac{q^2\overline{q}^b}{1-\overline{q}^b}$. However, to have an automaton for the bee, we need to have numbers in $\{1, 2, \ldots, M\}$. We therefore propose to see (y, b) as a convex combination of pure pairs $(y^*, b^*) \in \{1, 2, \ldots, M\}^2$ and to have the bee perform an initial randomization over the pure automata $A(y^*, b^*)$ according to the weights of the convex combination. Then, in expectation, the bee will leave Y after y consecutive failures and it will leave B after b consecutive failures. In view of the bee's bounded recall, it is worthwhile to notice that with $M = 2$ one can handle δ as small as 0.22, while with $M = 3$ one can handle δ as small as 0.18. Thus, for all $p, q \in [0.22, 0.78]$ one can obtain matching with automata $A(y, b)$ with $y, b \in \{1, 2\}$.

For a bee doing matching with an automaton of above type, the number of consecutive empty flowers it allows itself to encounter in yellow can be different from that in blue. One can think of the bee as having an internal mechanism by which, after some rough estimation of p and q, the natural numbers y^* and b^* are selected. It is not necessarily true that the bee can use an automaton of type $A(x, x)$ since there does not always exist a real number $x \geq 1$ with $\frac{p^2\overline{p}^x}{1-\overline{p}^x} = \frac{q^2\overline{q}^x}{1-\overline{q}^x}$. If for example one takes $p = 0.6$ and $q = 0.8$, then such x does not exist. However, we have the following result.

Theorem 3.4 *If $p \leq q \leq 1-p$, then there exists $x \geq 1$ such that*

$$\frac{p^2\overline{p}^x}{1-\overline{p}^x} = \frac{q^2\overline{q}^x}{1-\overline{q}^x}. \quad (10)$$

Proof: If $p = q$ or if $\overline{p} = q$, then one can take $x = 1$. Now let $p < q < \overline{p}$. Using an automaton $A(x, x)$ the ratio of the frequencies of visits to Y and B is (cf. example $A(3,2)$ above)

$$f(x,x) = \frac{q\overline{q}^x(1-\overline{p}^x)}{p\overline{p}^x(1-\overline{q}^x)}. \tag{11}$$

Then $\lim_{x\to\infty} f(x,x) = 0$ and $f(1,1) = \overline{q}/\overline{p} > p/q$. Hence, by continuity there exists $x \geq 1$ with $f(x,x) = p/q$, or equivalently $\frac{p^2\overline{p}^x}{1-\overline{p}^x} = \frac{q^2\overline{q}^x}{1-\overline{q}^x}$. □

Obviously a similar result can be obtained for $q \leq p \leq \overline{q}$. Remark that the condition of this theorem is easily satisfied if p and q are small. Such conditions are frequently observed in natural situations (Shreiber 1993).

Suppose we have finitely many bees foraging on two patches Y and B consisting of Bernoulli flowers. At Y each flower gives 1 unit of nectar with probability p. At B each flower is full with probability q. We assume that the nectar supply probabilities are independent of the numbers of visiting bees. If in this situation each individual bee determines, by its internal mechanism, an automaton to forage on Y and B, then each of these individuals will approximately spend $\frac{p}{p+q}$ of its foraging time on Y and $\frac{q}{p+q}$ on B. Even stronger, we can say that for each individual bee the probability of being at Y at time t converges to $\frac{p}{p+q}$. Thus, by the strong law of large numbers the fraction of the numbers of bees we encounter at Y at time t converges to $\frac{p}{p+q}$ as t and the number of bees increase. That is, a $\frac{p}{p+q}$-part of the bee population will be at Y, while the others, a $\frac{q}{p+q}$-part, will be at B for large t and a large number of bees. In other words, one would observe the ideal free distribution.

IFD with a continuum of bees

Consider a continuum of identical bees that are all using the failures strategy $A(r,s)$ with $r, s \in \mathbf{N}$, to forage on patches Y and B that have respectively total nectar supply y and b. The quantities are shared at each color

by the present bees. Given critical levels for the bees at Y and B, the "full-flower" probabilities, p and q respectively, are determined by the proportions of bees currently present in each of the patches. This population of bees can be distributed according to the IFD, i.e. there are full-flower probabilities p and q, and related critical levels, for Y an B respectively, such that each bee using $A(r,s)$ is matching p/q, while the ratio of the fractions of bees at Y and B is y/b. More formally:

Theorem 3.5 *If $y > b$ and $ys > br$, then there exist $p, q \in (0,1)$ such that*

$$\frac{y}{b} = f(r,s) = \frac{q\overline{q}^s(1-\overline{p}^r)}{p\overline{p}^r(1-\overline{q}^s)} = \frac{p}{q}. \tag{12}$$

Proof: For $q \in (0, b/y]$ define:

$$g(q) = \frac{(y/b)^2(1-qy/b)^r(1-(1-q)^s)}{(1-q)^s(1-(1-qy/b)^r)} \tag{13}$$

Then g is continuous on $(0, b/y]$ with $g(b/y) = 0$ and with

$$\begin{aligned} \lim_{q \downarrow 0} g(q) &= (y/b)^2 \lim_{q \downarrow 0} \tfrac{1-(1-q)^s}{1-(1-qy/b)^r} \\ &= (y/b)^2 \lim_{q \downarrow 0} \tfrac{s(1-q)^{s-1}}{(ry/b)(1-qy/b)^{r-1}} \\ &= \tfrac{(y/b)^2 s}{ry/b} = \tfrac{ys}{rb} > 1. \end{aligned} \tag{14}$$

By continuity of g there exists $q^* \in (0, b/y]$ with $g(q^*) = 1$. Now q^* and $p^* = yq^*/b$ are as desired. □

Note that this theorem is a static result for the existence of IFD with matching bees doing $A(r,s)$. The result does not provide a dynamic process of how to reach the IFD. We have to assume a continuum of bees in order to have p and q not being affected by single bees moving from one state of the automaton to another state of the automaton. The proportions of bees in the states of the automaton have to be independent of time. With a finite number of bees the probabilities p and q would always depend on the precise number of bees in those states.

Attitude Towards Risk

Consider the single-bee situation of foraging on two patches Y and B, where all flowers have a normally distributed nectar supply with a common mean μ. The yellow flowers have variance y, the blue ones have variance b.

Theorem 3.6 *Suppose the bee is using a failures strategy and has a fixed critical level cl. Without loss of generality assume $y < b$.*
If $cl < \mu$, then the bee will act as if it is risk averse, i.e. it will spend more time on Y than on B.
If $cl > \mu$, then the bee will act as if it is risk prone, i.e. it will spend more time on B than on Y.

Proof: If $cl < \mu$, then the probability of getting a full flower is larger for Y than for B (Figure 2 in Section 2). Hence the probability p of getting a full Y flower is larger than q for a B flower. Since the bee's mechanism will find an automaton to match p and q, the bee will spend more time in Y than in B. The second part is similar. □

Remark that this result can also be extended to apply to other nectar distribution functions, like the ones discussed for the ε-sampling strategy.

Finally for this section we like to remark that we have only considered finite automata of the type: leave Y (B) after y (b) consecutive failures. However, one could also examine automata of a more general type. Let S, S_Y and S_B be finite non-empty sets of states with $S = S_Y \cup S_B$ and $S_Y \cap S_B = \phi$. We can describe a foraging automaton for the bee as a map $T : S \times \{0,1\} \to S$ with the interpretation that a bee in state $s \in S_Y$ is visiting a yellow flower; if this particular yellow flower is full (empty) then the bee moves to state $T(s,1)$ (resp. $T(s,0)$). Further research is required to fully understand the possibilities of obtaining matching and IFD results by means of these general type foraging automata.

4 Discussion and Related Literature

The Matching Law

Many studies, articles, and even special books have been devoted to the phenomena of "the Matching Law." (Some main and recent references are Simon 1956, Herrenstein 1970, Heyman 1979, Commons et al. 1982, Houston et al. 1982, Houston 1983, Staddon 1983, Davison & McCarthy 1988, Staddon & Horner 1989). The reader of the above literature will probably be confused (as we are) by the rich and complicated details of the experimental results as well as by the theoretical analyses. There are very many versions of the matching law mathematical function (compare for example Krebs & Kacelnik 1991 to Houston & Sumida 1987 to Davison & McCarthy 1988 to the commentary by Herrenstein & Vaughan in Maynard Smith 1984).

In this study we focussed on one main issue related to the matching law: why the animal in an artificial binary choice setting behaves "irrationaly" and does not go exclusively to the resource with the higher probability? Instead, the matching law reveals (Krebs & Kacelnik 1991) that the animal allocates its long-run behavior to two alternatives in proportion to the reward it obtains from them. To answer this question, we presented boundedly rational strategies for which the irrational matching behavior is compatible with the equilibrium conditions of the natural IFD.

We have presented foraging rules that lead the forager to match over time the reward probabilities by the fractions of the visits to the alternatives. However, one should not confuse this matching law with "probability matching" (Maynard Smith 1984). Probability matching is a foraging rule where, at each point in time, the forager is choosing an alternative according to the observed full flower probabilities at the respective patches. While probability matching is a moment-to-moment foraging rule, the matching

law describes the average behavior of the forager over an asymptotically long period of time.

Learning Rules

As Maynard Smith (1984) points out, a learning rule (i.e. a foraging strategy) that we observe in animals should have several properties:

a. It should have the *relative payoff sum* (RPS) property, which says that, after a sufficiently long period of time, the probability of doing a certain act should equal the total payoff received so far for doing this act, divided by the total payoff received so far for all acts.

b. None of the available acts should ever fall to zero probability, since the environment might change.

c. Any naive animal should start with some prior probabilities of performing the different acts.

d. Recent payoffs should have a bigger effect on behavior than early ones (discount factor).

A strategy having these properties is Harley's RPS rule (Harley 1981, Maynard Smith 1984). For a two-choices situation (Y, B) this rule is defined as follows (Harley 1981):
Let $r_Y, r_B > 0$ (residual values) and let $0 < x < 1$ (memory factor). Let $P_i(t)$ denote the payoff in $i \in \{Y, B\}$ at time $t \in \mathbf{N}$. Now let $S_i(0) = r_i$ and for $t \geq 1$ define

$$S_i(t) = xS_i(t-1) + (1-x)r_i + P_i(t). \tag{15}$$

At time t choose alternative $i \in \{Y, B\}$ with probability

$$f_i(t) = \frac{S_i(t-1)}{S_Y(t-1) + S_B(t-1)} \tag{16}$$

"In words, the (this) RPS rule says the following: display most frequently the behaviour which has, up to the present, paid the most, but only in proportion, roughly, to its cumulative payoff relative to the overall total" (Harley 1981). Although this rule is fairly simple, the foraging animal is required to adjust its probablities of choosing either Y or B at each point in time. Compared to it we have presented an explicit "molecular" ("moment to moment" in Krebs & Kacelnik 1991 terms) strategy that has the above properties, but for which the foraging animal will only switch every once in a while. Notice that Harley's rule assumes the animal to update probabilities at all time points and chooses Y or B independent of the patch it is currently visiting. We do not believe that bees are capable of updating and computing probabilities before each visit (10 to 40 visits per minute!). Our foraging strategies give the same results while the bee is following very simple movement rules.

Milinski Fishes

Our ε-sampling strategy explains explicitly the dynamics in which "Milinski fishes" reach the IFD (Milinski 1979, 1984, Godin & Keenleside 1984, Milinski & Parker 1991). Each fish has to remember only an estimate of the average payoff received so far in the old resource, and to compare it with the current payoff in the new food source when sampling. If the current payoff is higher, the fish stays; if it is lower, it goes back to the old food source. This biological behavior corresponds to the potential function of Monderer & Shapley (1988). Milinski & Parker (1991, page 144) have a stationary model of the IFD with foraging fishes, but they do not have an explicit dynamic model by which the fishes can reach the IFD. Their model (including Parker & Sutherland 1986) can be viewed as a special case of the short-run stable matching of Peleg & Shmida (1992) where the fishes' different competitive weights correspond to the bees' different handling times

(technological abilities, sensu Selten 1978).

Godin & Keenleside (1984) have shown experimentally that the IFD can be achieved through "sampling." However, no explicit strategy has been suggested in the literature of how fish carried out the sampling procedure. Our ε-sampling strategy corresponds to the "Major-Minor behavior" of bees, which has been observed in bumblebees by Heinrich (1979). The bumblebee visits mainly a certain flower type, the major one, but once in a while it samples (doing minoring) other flower types. It would be interesting to investigate how an indivdual bee's parameter ε is influenced by its life history and its environment.

Milinski (1984) and Godin & Keenleside (1984) received interesting results when comparing the switching rate between two resources of fish with different competitive ability: Individuals experiencing a high feeding rate (high payoff) tend to switch patches less frequently than those individuals that received lower payoffs. These results can be explained by our ε-sampling strategy (and also by the failure strategy). The fishes which are receiving less, reach the threshhold of leaving more frequently, and the initiative to sample somewhere else is greater when ε-sampling is payoff dependent (with ε increasing with low payoffs and decreasing with high payoffs).

Attitude Towards Risk

Our model explains in a simple way (without the need of utility theory) the well-known pattern in animal behavior of risk aversion and risk proneness (Real & Caraco 1986, Stephens & Krebs 1986, Krebs & Kacelnik 1991, McNamara & Houston 1992): In an environment in which the resource is normally distributed, the critical level can be interpreted as an existing condition for the animal. If the critical level is below the resource mean (Figure 2), then the animals should behave as if they are risk averse, while

if the critical level is above the mean, then they should behave as if they are risk prone. Our model predicts only a tendency to visit one of the resources more frequently and not to make an exclusive choice for one of the resources. In the case where nectar is distributed as in Figure 3, no matter what its critical level is, the bee will prefer the blue flower.

The elucidated review on risk sensitivity by McNamara & Houston (1992) has technically similar results to our points on attitude towards risk. However, they ask themselves which alternative the animal would prefer, while we find out what would happen to the animal if we take into account the observations of IFD and matching. In their model the critical level is a kind of evolutionary knowledge which, in a sense uses complete information about the environment. In our model the animal's actions are governed only by its own recent experiences and no complete information is required.

Bounded Rationality and Myopic Learning

Our approach to studying foraging behavior is quite different from the "optimal foraging theory" used in ecology (Pyke et al. 1977, Krebs & Kacelnik 1991, Stephens & Krebs 1986, Bernstein et al. 1988). In optimal foraging theory the decision to leave a patch (resource alternative) is based on a comparison to the surroundings, in other words, it assumes that the animal has complete information and a powerful memory and computational ability. Our basic approach is that the animal uses "bounded memory" and makes its decisions only on the basis of its own recent experience. It does not know its competitor's moves/payoffs. It even may not know that it is involved in a game situation. The animal uses very simple decision rules to decide when to leave a patch (flower type), to decide where to go, and to decide whether or not to stay at the "new" patch. In such very fast biological activities (one bee makes very many visits per minute) the

animals use mainly their short term memory (Menzel 1985, 1990) and the movement rules depend on very short recall (e.g. remember the last 1-3 flowers) and very simple calculations (Real et al. 1990, Real 1991, 1992). These issues are related to myopic learning models (Monderer & Shapley 1988, Fudenberg & Kreps 1991, Milgrom & Roberts 1991, Monderer & Sela 1993) and to theory on bounded rationality (Kalai 1988, Selten 1990, Aumann 1992). We believe that bees and most other animals are not able to do sophisticated calculation of probabilities (e.g. as in the RPS-rule of Harley (1981), the learning rule by McNamara & Houston (1985) or in learning rules that require bayesian updating) and can neither update expected payoffs by functions that comprise long recall of history. Of course, in a matching experiment the reward probabilities are not known to the bee; these are known only to the researcher. One of the main limitations of many of the previous models is that they analyze the situation as if the bee does know those probabilities.

This bounded rationality approach is explained nicely in Boyd & Richerson 1985 (p. 93) when they address the issue of how animals and people apply Bayesian rationality: "simple rules of thumb (... called heuristics by psychologists) may greatly reduce cognitive complexity of decisions but still result in behavior that closely approximates normatively rational behavior in some restricted range of environments ... These heuristics often work well but occasionally lead to behavior that is irrational according to canons of Bayesian rationality."

In the foregoing pages we have presented an explicit model in which simple decision rules, that need only very short recall and only elementary calculations, can dictate an optimal foraging strategy. We have seen that finite automata with very few states appear to be appropriate tools for such tasks (Ben-Porath 1991, Ben-Porath & Peleg 1987). Our model stands in agreement with recent experiments of foraging animals which reveal that

animals take into account only the last 1-3 rewards when making short-term decisions (sensu Menzel 1990). It also fits the "melioration approach" (Herrenstein & Vaughan 1980) that animals use very simple choice rules which lead them to behave (sub)optimally in very complex natural situations (Houston et al. 1982, Hinson & Staddon 1983 and Boyd & Richerson 1985). To an outside observer this simple behavior looks very sophisticated and complicated as if they use utility functions, probability updating and complicated calculus. We believe that the same approach can explain some "irrational" behavior in economics and sociology; some "bounded rational" - ad hoc - strategies that are optimal under particular natural conditions may look very irrational in artificial situations. This is illustrated by the comparison of the matching experiment and the IFD phenomenon in nature.

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